

Status and Trends of Prey Fish Populations in Lake Michigan, 2013¹

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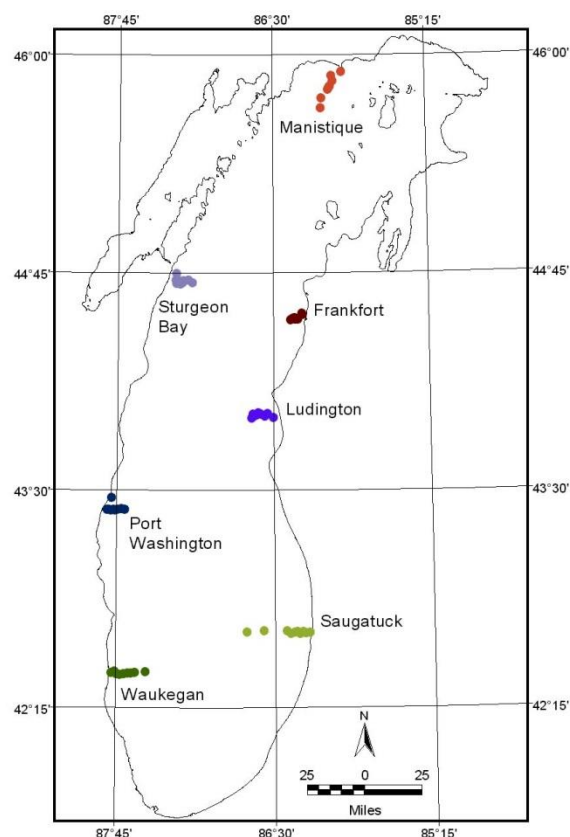
Abstract

The U.S. Geological Survey Great Lakes Science Center has conducted lake-wide surveys of the fish community in Lake Michigan each fall since 1973 using standard 12-m bottom trawls towed along contour at depths of 9 to 110 m at each of seven index transects. The resulting data on relative abundance, size and age structure, and condition of individual fishes are used to estimate various population parameters that are in turn used by state and tribal agencies in managing Lake Michigan fish stocks. All seven established index transects of the survey were completed in 2013. The survey provides relative abundance and biomass estimates between the 5-m and 114-m depth contours of the lake (herein, lake-wide) for prey fish populations, as well as burbot, yellow perch, and the introduced dreissenid mussels. Lake-wide biomass of alewives in 2013 was estimated at 29 kilotonnes (kt, 1 kt = 1000 metric tonnes), which was more than three times the 2012 estimate. However, the unusually high standard error associated with the 2013 estimate indicated no significant increase in lake-wide biomass between 2012 and 2013. Moreover, the age distribution of alewives remained truncated with no alewife exceeding an age of 5. The population of age-1 and older alewives was dominated (i.e., 88%) by the 2010 and 2012 year-classes. Record low biomass was observed for deepwater sculpin (1.3 kt) and ninespine stickleback (0.004 kt) in 2013, while bloater (1.6 kt) and rainbow smelt (0.2 kt) biomasses remained at low levels. Slimy sculpin lake-wide biomass was 0.32 kt in 2013, marking the fourth consecutive year of a decline. The 2013 biomass of round goby was estimated at 10.9 kt, which represented the peak estimate to date. Burbot lake-wide biomass (0.4 kt in 2013) has remained below 3 kt since 2001. Numeric density of age-0 yellow perch (i.e., < 100 mm) was only 1 fish per ha, which is indicative of a relatively poor year-class. Lake-wide biomass estimate of dreissenid mussels in 2013 was 23.2 kt. Overall, the total lake-wide prey fish biomass estimate (sum of alewife, bloater, rainbow smelt, deepwater sculpin, slimy sculpin, round goby, and ninespine stickleback) in 2013 was 43 kt, with alewives and round gobies constituting 92% of this total.

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The U.S. Geological Survey Great Lakes Science Center (GLSC) has conducted daytime bottom trawl surveys in Lake Michigan during the fall annually since 1973. Estimates from the 1998 survey are not reported, however, given the trawls were towed at non-standard speeds. From these surveys, the relative abundance of the prey fish populations are measured, and estimates of lake-wide biomass available to the bottom trawls (for the region of the main basin between the 5-m and 114-m depth contours) can be generated (Hatch et al. 1981; Brown and Stedman 1995). Such estimates are critical to fisheries managers making decisions on stocking and harvest rates of salmonines and allowable harvests of fish by commercial fishing operations.

The basic unit of sampling in our surveys is a 10-minute tow using a bottom trawl (12-m headrope) dragged on contour at 9-m (5 fathom) depth increments. At most survey locations, towing depths range from 9 or 18 m to 110 m. Age determinations were estimated for alewives (*Alosa pseudoharengus*, using otoliths) and bloaters (*Coregonus hoyi*, using scales) from our bottom trawl catches (Madenjian et al. 2003; Bunnell et al. 2006a). Although our surveys have included as many as nine index transects in any given year, we have consistently conducted the surveys at seven transects. These transects are situated off Manistique, Frankfort, Ludington, and Saugatuck, Michigan; Waukegan, Illinois; and Port Washington and Sturgeon Bay, Wisconsin (Figure 1). All seven transects were completed in 2013.



Lake-wide estimates of fish biomass require (1) accurate measures of the surface areas that represent the depths sampled and (2) reliable measures of bottom area swept by the trawl. A complete Geographical Information System (GIS) based on depth soundings at 2-km intervals in Lake Michigan was developed as part of the acoustics study performed by Argyle et al. (1998). This GIS database was used to estimate the surface area for each individual depth zone surveyed by the bottom trawls. Trawl mensuration gear that monitored net configuration during deployment revealed that fishing depth (D , in meters) influenced the bottom area swept by the trawl. We have corrected the width (W , in meters) of the area sampled according to $W = 3.232 + 7.678(1 - e^{-0.044 \cdot D})$, as well as the actual time (AT , in minutes) spent on the bottom according to $AT = \text{tow time} - 0.945 + (0.056D)$, based on trawl measurements made during June 2009 (Madenjian et al. 2010a). These relationships, along with boat speed, were used to estimate bottom area swept.

Figure 1. Established sampling locations for GLSC bottom trawls in Lake Michigan.

We estimate both numeric (fish per hectare [ha]) and biomass (kg per ha) density, although we display graphical trends mostly in biomass for brevity. A weighted mean density over the entire range of depths sampled (within the 5-m to 114-m depth contours) was estimated by first calculating mean density for each depth zone, and then weighting mean density for each depth zone by the proportion of lake surface area assigned to that depth zone. Standard error (SE) of mean density was estimated by weighting the variances of fish density in each of the depth zones by the appropriate weight (squared proportion of surface area in the depth zone), averaging the weighted variances over all depth zones, and taking the square root of the result.

NUMERIC AND BIOMASS DENSITY BY SPECIES

By convention, we classify "adult" prey fish as age 1 or older, based on total length (TL): alewives ≥ 100 mm, rainbow smelt (*Osmerus mordax*) ≥ 90 mm, bloaters ≥ 120 mm, and yellow perch (*Perca flavescens*) ≥ 100 mm. We assume all fish smaller than the above length cut-offs are age-0; length cut-offs are also aided by aging of alewife (by otoliths) and bloater (by scales). Catches of age-0 alewife are not reliable indicators of future year-class strength (Madenjian et al. 2005a), because their position in the water column makes them less vulnerable to bottom trawls. Catches of age-0 bloater, though biased low, can be used as an index of relative abundance given the positive correlation between density of age-0 bloater and density of age-3 bloater (the age at which catch curves reveal full recruitment to our gear, Bunnell et al. 2006a, 2010). Catch of age-0 yellow perch is likely a good indicator of year-class strength, given that large catches in the bottom trawl during the 1980s corresponded to the strong yellow perch fishery. At the end of this report, we report densities of age-0 yellow perch and other bottom-dwelling species such as burbot (*Lota lota*) and dreissenid mussels that are not necessarily "prey fish" but are caught in sufficient numbers to index. Unfortunately lake whitefish (*Coregonus clupeaformis*) are only rarely sampled in our trawl and the resultant trends are not meaningful.

Alewife – Since its establishment in the 1950s, the alewife has become a key member of the fish community. As a larval predator, adult alewife can depress recruitment of native fishes, including burbot, deepwater sculpin (*Myoxocephalus thompsonii*), emerald shiner (*Notropis atherinoides*), lake trout (*Salvelinus namaycush*), and yellow perch (Smith 1970; Wells and McLain 1973; Madenjian et al. 2005b, 2008; Bunnell et al. 2006b). Additionally, alewife has remained the most important constituent of salmonine diet in Lake Michigan for the last 45 years (Jude et al. 1987; Stewart and Ibarra 1991; Warner et al. 2008; Jacobs et al. 2013). Most of the alewives consumed by salmonines in Lake Michigan are eaten by Chinook salmon (*Oncorhynchus tshawytscha*, Madenjian et al. 2002). A commercial harvest was established in Wisconsin waters of Lake Michigan in the 1960s to make use of the then extremely abundant alewife that had become a nuisance and health hazard along the lakeshore. In 1986, a quota was implemented, and as a result of these restrictions, the estimated annual alewife harvest declined from about 7,600 metric tons in 1985 to an incidental harvest of only 12 metric tons after 1990 (Mike Toney, Wisconsin Department of Natural Resources, Sturgeon Bay, personnel communication). Lake Michigan currently has no commercial fishery for alewives.

According to the bottom trawl survey results, adult alewife biomass density increased from 1.4 kg per ha in 2012 to 8.2 kg/ha in 2013 (Figure 2a). However, the unusually high standard error associated with the 2013 density estimate indicated no significant increase in biomass density between the two years. Similarly, adult alewife numeric density increased from 64 fish/ha in 2012 to 417 fish/ha in 2013 (Figure 2b), but the unusually high standard error associated with the 2013 density estimate indicated no

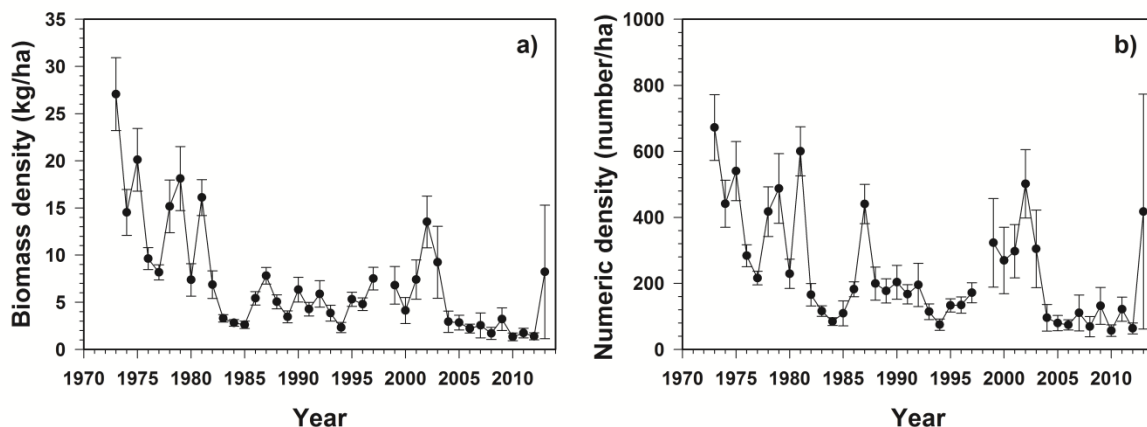


Figure 2. Density of adult alewives as biomass (a) and number (b) per ha (+/- standard error) in Lake Michigan, 1973-2013.

significant increase in numeric density between the two years. These high standard errors were primarily due to one relatively high catch of adult alewives at the 9-m depth at Saugatuck.

Given the extremely high standard errors for the 2013 estimates, adult alewife biomass density has appeared to remain at a low level during 2004-2013 (Figure 2). This continued depression of adult alewife abundance may reflect a recently intensified amount of predation exerted on the alewife population by Chinook salmon due to four factors: (1) a relatively high percentage of wild Chinook salmon in Lake Michigan (averaging 50% age-1 individuals between 2006-2010, Williams 2012), (2) increased migration of Chinook salmon from Lake Huron in search of alewives (Adlerstein et al. 2007; R. Clark, Michigan State University Quantitative Fisheries Center, personal communication), (3) increased importance of alewives in the diet of Chinook salmon in Lake Michigan between the 1990s and the 2000s (Jacobs et al. 2013), and (4) a decrease in the energy density of adult alewives during the late 1990s (Madenjian et al. 2006). The long-term temporal trends in adult alewife biomass, as well as in alewife recruitment to age 3, in Lake Michigan are attributable to consumption of alewives by salmonines (Madenjian et al. 2002, 2005a; Tsehaye et al. 2014).

We estimated that 41% and 47% of adult alewives captured in the bottom trawl during 2013 were age-1 and age-3 fish, respectively (Figure 3). Of the 314 alewives aged from the 2013 bottom trawl survey, only 8 and 6 alewives were age-4 and age-5 fish, respectively, and none of these 314 alewives were older than 5 years old. Thus, the recent trend of age truncation in alewife population age structure continued in 2013, with the oldest alewife being only 5 years old (Figure 3). Prior to 2008, age-8 alewives were routinely captured.

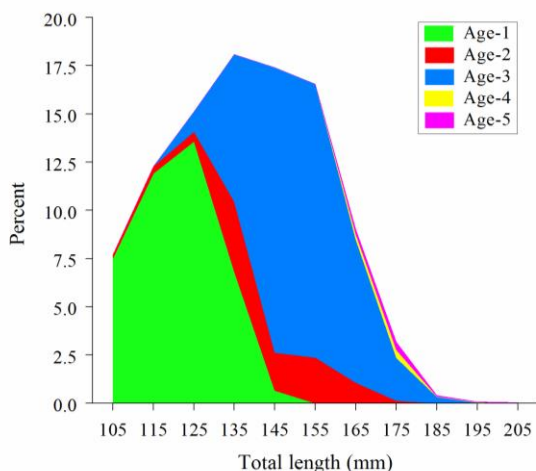


Figure 3. Age-length distribution of alewives ≥ 100 mm total length caught in bottom trawls in Lake Michigan, 2013. Note that smaller alewives were captured but were not included herein.

Our results for temporal trends in adult alewife density were in general agreement with results from the lake-wide acoustic survey, which reported biomass of adult alewife during 2004-2013 to be relatively low in comparison to the biomass during 1994-1996 (Warner et al. 2014). However, Warner et al. (2014) did report a substantial increase in adult alewife biomass during 2007-2010 that was not detected by the

bottom trawl survey. On average, for adult alewife biomass density, the acoustic estimate exceeded the bottom trawl estimate by a factor of three to four. But, in 2013, the acoustic estimate (5.0 kg/ha) was not significantly different from the bottom trawl estimate (8.2 kg/ha).

Bloater - Bloaters are eaten by salmonines in Lake Michigan, but are far less prevalent in salmonine diets than alewives (Warner et al. 2008; Jacobs et al. 2010, 2013). For large (≥ 600 mm) lake trout, over 30% of the diets offshore of Saugatuck and on Sheboygan Reef were composed of adult bloaters during 1994-1995, although adult bloaters were a minor component of lake trout diet at Sturgeon Bay (Madenjian et al. 1998). For Chinook salmon, the importance of bloater (by wet weight) in the diets has declined between 1994-1995 and 2009-2010. For small (< 500 mm) Chinook salmon the proportion declined from 9% to 6% and for large Chinook salmon the proportion declined from 14% to $<1\%$ (Jacobs et al. 2013). The bloater population in Lake Michigan also supports a valuable commercial fishery, although its yield has generally been declining since the late 1990s.

Although adult bloater biomass density increased from 0.11 kg per ha in 2012 to 0.41 kg per ha in 2013, adult bloater biomass density in the Lake Michigan, based on our survey results, has remained at a

relatively low level for nearly a decade (Figure 4a). These low biomass densities represent a continuation of an overall declining trend since 1989 (Figure 4a). Numeric density of age-0 bloaters (< 120 mm TL) was only 6 fish per ha in 2013 (Figure 4b), thus 2013 was the fourth consecutive year of very low densities of age-0 bloater following relatively high values in 2005, 2008, and 2009.

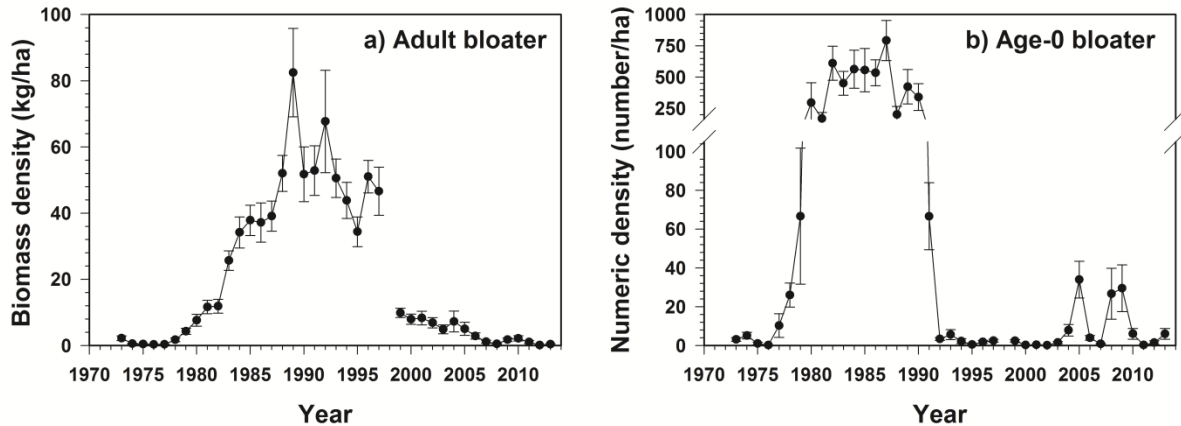


Figure 4. Panel (a) depicts biomass density (\pm standard error) of adult bloater in Lake Michigan, 1973-2013. Panel (b) depicts numeric density (\pm standard error) of age-0 bloater in Lake Michigan, 1973-2013.

The exact mechanisms underlying the relatively poor bloater recruitment since 1992, and the resultant low biomass of adult bloater, remain unknown. Of the mechanisms that have been recently evaluated, reductions in fecundity associated with poorer condition (Bunnell et al. 2009a) and egg predation by slimy and deepwater sculpins (Bunnell et al. 2014) are likely contributing to the reduced bloater recruitment, but none is the primary regulating factor. Another hypothesized mechanism, predation by adult alewife on bloater larvae, has been discounted (Madenjian et al. 2002; Bunnell et al. 2006a). Madenjian et al. (2002) proposed that the Lake Michigan bloater population may be cycling in abundance, with a period of about 30 years, although the exact mechanism by which recruitment is regulated remains unknown. Finally, a regional climate driver was hypothesized to underlie the synchrony in bloater recruitment among lakes Michigan, Huron, and Superior between 1978 and 2006 (Bunnell et al. 2010).

One additional consideration when interpreting these bottom trawl survey results is that bloater catchability may have decreased in recent years, in response to the proliferation of quagga mussels and the associated increased water clarity and decreased *Diporeia* spp. densities. Specifically, a substantial portion of the bloater population in Lake Michigan may have shifted to waters deeper than those typically surveyed by the GLSC. In support of this contention, we note that bloaters have exhibited plasticity in the bottom depths that they occupy, as the depth at which their peak densities occurred increased from 50 m in the 1930s to 85-110 m by 2004-2007 (Bunnell et al. 2012). In addition, commercial fishers have reported an increase in the depth at which they catch bloaters in Lake Michigan during the past 5 to 10 years, with the bulk of the catch from waters deeper than 130 m during recent years (M. LeClair, Susie-Q Fish Market, Two Rivers, WI, personal communication; D. McMurry, Big Stone Bay Fishery, Inc., Carp Lake, MI, personal communication). As a preliminary investigation of this movement-to-deeper-water hypothesis, we performed a bottom trawl tow at a bottom depth between 128 and 132 m at each of the Manistique, Frankfort, and Port Washington transects during 2013. No bloaters were caught in these three tows. Nevertheless, the bulk of the adult bloater population in Lake Michigan may still have been in waters deeper than 130 m during the recent bottom trawl surveys, given the reports from the commercial fishers.

In terms of comparing trends between the two surveys of Lake Michigan, for adult bloater, an order of magnitude decrease between 1992-1996 and 2001-2013 was revealed by both surveys. Similarly, low densities of age-0 bloaters in the 1990s and strong interannual variability in the 2000s were detected in both surveys. However, the years (2005, 2008, 2009) in which relatively high age-0 densities were

estimated by the bottom trawl survey were a subset of the high density years (2001, 2005, 2007-2009, 2012) estimated by the acoustic survey (Warner et al. 2014).

Rainbow smelt – Adult rainbow smelt are an important part of the diet for intermediate-sized (400 to 600 mm) lake trout in the nearshore waters of Lake Michigan (Stewart et al. 1983; Madenjian et al. 1998; Jacobs et al. 2010). For Chinook salmon, rainbow smelt comprised as much as 18% in the diets of small individuals in 1994-1996, but that dropped precipitously to 2% in 2009-2010 and rainbow smelt has been consistently rare in the diets of larger Chinook salmon since 1994 (Jacobs et al. 2013). The rainbow smelt population supports commercial fisheries in Wisconsin and Michigan waters (Belonger et al. 1998; P. Schneeberger, Michigan Department of Natural Resources, Marquette, MI, personal communication).

Despite the nominal increase in adult rainbow smelt biomass density from 0.02 kg per ha in 2012 to 0.05 kg per ha in 2013, adult rainbow smelt biomass density has remained at low levels since 2006 (Figure 5a). Adult rainbow smelt biomass density was highest from 1981 to 1993, but then declined between 1993 and 2001, and has remained at a relatively low density, except in 2005, since 2001. Age-0 rainbow smelt numeric density has been highly variable since 2002 (Figure 5b). Age-0 numeric density in 2013 was 11 fish per ha, which was only 6% of the long-term average. Causes for the general decline in rainbow smelt biomass and production remain unclear. Consumption of rainbow smelt by salmonines was higher in the mid 1980s than during the 1990s (Madenjian et al. 2002), yet adult and age-0 (< 90 mm TL) rainbow smelt abundance remained high during the 1980s (Figure 5b). Results from a recent population modeling exercise suggested that predation by salmonines was not the primary driver of long-term temporal trends in Lake Michigan rainbow smelt abundance (Tsehaye et al. 2014).

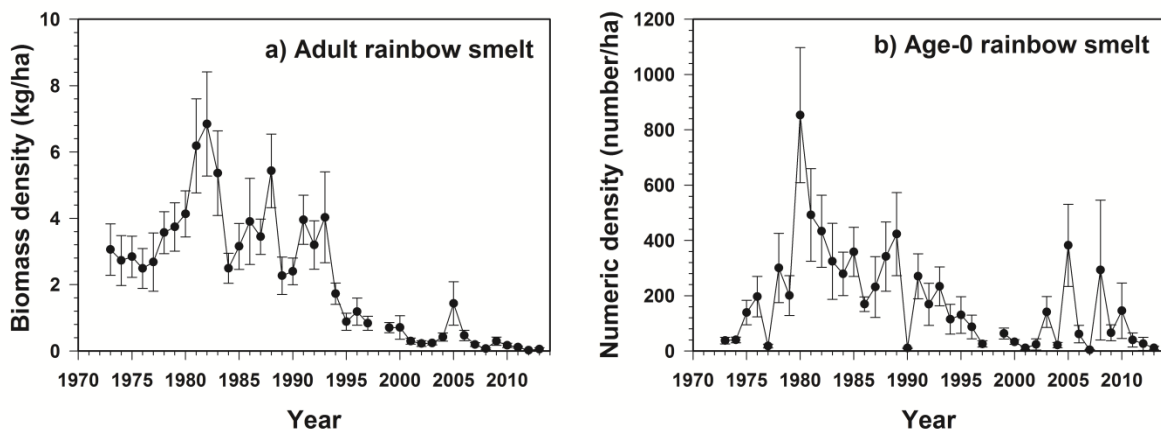


Figure 5. Biomass density (+/- standard error) of adult (a) and age-0 (b) rainbow smelt in Lake Michigan, 1973-2013.

Temporal trends in rainbow smelt biomass from the acoustic and bottom trawl surveys in Lake Michigan have been similar since 2001. The bottom trawl survey has documented relatively low rainbow smelt biomass during 2001-2013, with a minor peak in 2005 (Figure 5a). Similarly, biomass of rainbow smelt in the acoustic survey was relatively low during 2001-2013, with minor peaks occurring during 2005-2006 and 2008-2009 (Warner et al. 2014). Results from both the acoustic and bottom trawl surveys indicated that rainbow smelt biomass in Lake Michigan during 1992-1996 was roughly four times higher than rainbow smelt biomass during 2001-2013.

Sculpins – From a biomass perspective, the cottid populations in Lake Michigan have been dominated by deepwater sculpins, and to a lesser degree, slimy sculpins (*Cottus cognatus*). Spoonhead sculpins (*Cottus ricei*), once fairly common, suffered declines to become rare to absent by the mid 1970s (Eck and Wells 1987). Spoonhead sculpins were encountered in small numbers in our survey between 1990 and 1999 (e.g., Potter and Fleischer 1992), but have not been sampled since 1999.

Slimy sculpin is a favored prey of juvenile lake trout in nearshore regions of the lake (Stewart et al. 1983; Madenjian et al. 1998), but is only a minor part of adult lake trout diets. When abundant, deepwater sculpin can be an important diet constituent for burbot in Lake Michigan, especially in deeper waters (Van Oosten and Deason 1938; Brown and Stedman 1995; Fratt et al. 1997).

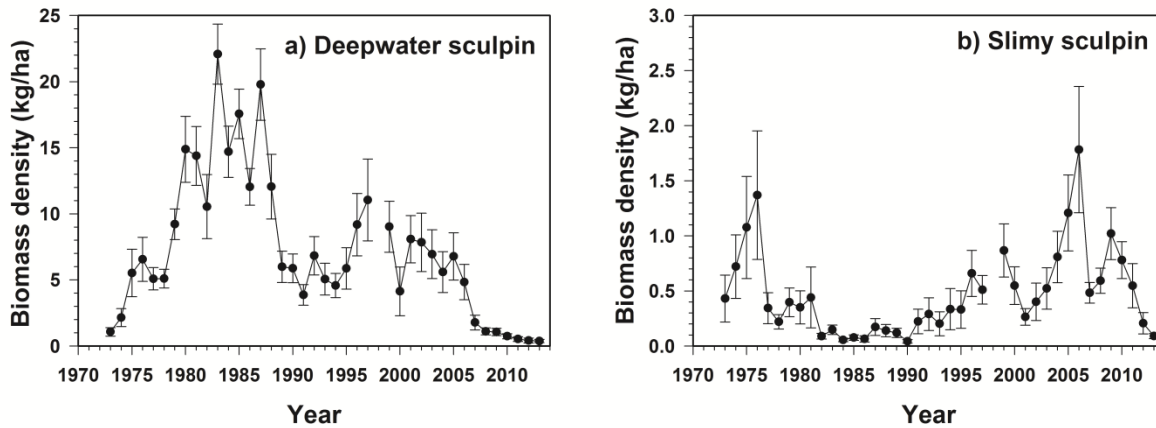


Figure 6. Biomass density (+/- standard error) for deepwater (a) and slimy sculpin (b) in Lake Michigan, 1973-2013.

Deepwater sculpin biomass density was 0.38 kg per ha in 2013 (Figure 6a), which was only 5% of the long-term average biomass and the lowest estimate of the time series. For every year since 2009, this biomass estimate has reached a record low. During 1990-2005, both deepwater sculpin biomass density and numeric density trended neither downward nor upward. However, biomass of deepwater sculpin sampled in the bottom trawl has declined precipitously since 2005. Madenjian and Bunnell (2008) demonstrated that deepwater sculpins have been captured at increasingly greater depths since the 1980s. Therefore, one potential explanation for the recent declines in deepwater sculpin densities is that an increasing proportion of the population is now occupying depths deeper than those sampled by our survey (i.e., 110 m). Furthermore, because the deepwater sculpin has historically occupied deeper depths than any of the other prey fishes of Lake Michigan, a shift to waters deeper than 110 m would seem to be a reasonable explanation for the recent declines in deepwater sculpin densities. Moreover, this explanation was supported by data from the additional trawl tows at bottom depths between 128 and 132 m during 2013. At each of these three transects (Manistique, Frankfort, Port Washington), the maximum deepwater sculpin biomass density occurred at the bottom depths between 128 and 132 m. Previous analysis of the time series indicated deepwater sculpin density is negatively influenced by alewife (predation on sculpin larvae) and burbot (predation on juvenile and adult sculpin, Madenjian et al. 2005b). Based on bottom trawl survey results, neither alewife nor burbot significantly increased in abundance during 2007-2013 to account for this decline in deepwater sculpins. Which factor or factors could have driven the bulk of the deepwater sculpin population to move to waters deeper than 110 m during 2007-2011? This shift to deeper water by deepwater sculpins coincided with the population explosion of the profundal form of the quagga mussel (*Dreissena rostriformis*) in depths between 60 and 90 m (Bunnell et al. 2009b; T. Nalepa, NOAA Great Lakes Environmental Research Laboratory, personal communication). Perhaps some consequences of the colonization of deeper waters by quagga mussels prompted a move of deepwater sculpins to deeper water. If this hypothesis were correct, then a substantial decline in quagga mussel abundance in the 60-m to 90-m deep waters could lead to a shift of deepwater sculpins back to shallower waters.

Slimy sculpin biomass density was 0.09 kg per ha in 2013, marking the fourth consecutive year of a decline (Figure 6b). Biomass density of slimy sculpins in 2013 approached the minimal levels observed during 1984-1986 and 1990. Slimy sculpin abundance in Lake Michigan appeared to be regulated, at least in part, by predation from juvenile lake trout (Madenjian et al. 2005b). We attribute the slimy sculpin recovery that occurred during the 1990s to, in part, the 1986 decision to emphasize stocking lake trout on offshore reefs (as opposed to the nearshore areas where our survey samples, Madenjian et al.

2002). Likewise, the slimy sculpin decline since 2009 coincided with a substantial increase in the rate of stocking juvenile lake trout into Lake Michigan (FWS/GLFC 2010).

Round goby – The round goby (*Neogobius melanostomus*) is an invader from the Black and Caspian Seas. Round gobies have been observed in bays and harbors of Lake Michigan since 1993, and were captured in the southern main basin of the lake as early as 1997 (Clapp et al. 2001). Round gobies were not captured in the GLSC bottom trawl survey until 2003, however. By 2002, round gobies had become an integral component of yellow perch diet at nearshore sites (i.e., < 15 m depth) in southern Lake Michigan (Truemper et al. 2006). Round gobies also had become an important constituent of the diet of burbot in northern Lake Michigan by 2005 (Hensler et al. 2008; Jacobs et al. 2010). Round gobies are also fed upon by smallmouth bass (*Micropterus dolomieu*) and lake trout, and more recently by lake whitefish, in Lake Michigan (T. Galarowicz, Central Michigan University, personal communication; McKenna 2014; S. Hansen, Wisconsin DNR, personal communication).

Round goby biomass density exhibited a peak value of 3.1 kg per ha in 2013; however, there was an unusually high degree of uncertainty, arising from the bulk of the round gobies being caught in a single trawl tow at the 18-m depth at Waukegan, associated with this estimate (Figure 7a). In general, standard errors associated with the reported mean biomass densities for round goby were relatively high. Given this high degree of uncertainty, round goby abundance in Lake Michigan may already be leveling off in response to control by piscivores. This hypothesis was supported by the round goby mortality estimates by Huo et al (2014), who estimated that round gobies in the main basin of Lake Michigan are experiencing annual mortality rates of between 75 and 85%, which are comparable to the mortality rates currently experienced by Lake Michigan adult alewives (Tsehaye et al. 2014).

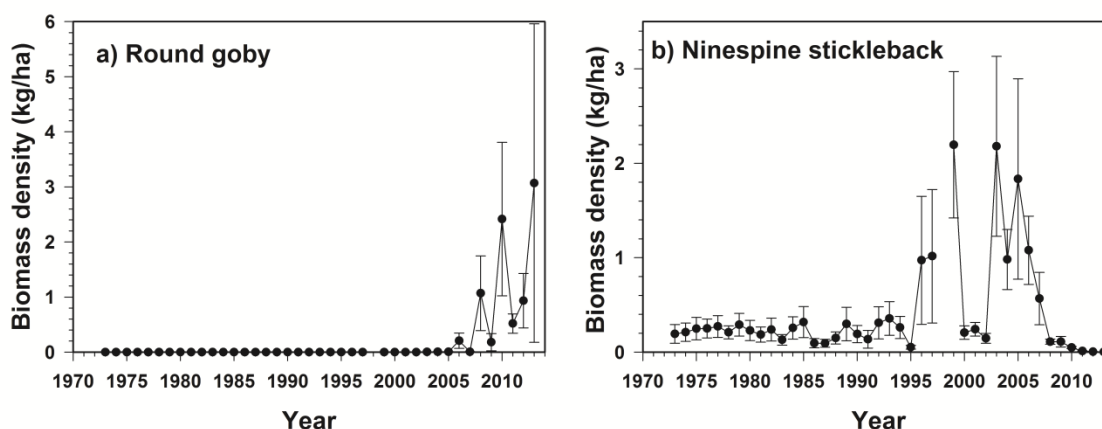


Figure 7. Biomass density (+/- standard error) of round goby (a) and ninespine stickleback (b) in Lake Michigan, 1973-2013.

Ninespine stickleback – Two stickleback species occur in Lake Michigan. Ninespine stickleback (*Pungitius pungitius*) is native, whereas threespine stickleback (*Gasterosteus aculeatus*) is non-native and was first collected in the GLSC bottom trawl survey during 1984 (Stedman and Bowen 1985). Ninespine stickleback is generally captured in far greater densities than the threespine. Relative to other prey fishes, ninespine sticklebacks are of minor importance to lake trout and other salmonines. In northern Lake Michigan, for example, sticklebacks occur infrequently in the diet of lake trout (Elliott et al. 1996; Jacobs et al. 2010). Biomass density was only 1 g per ha in 2013 (Figure 7b), the lowest value of the time series and only 0.3% of the long-term average. Biomass of ninespine stickleback remained fairly low from 1973-1995, increased dramatically in 1996-1997, and exhibited larger interannual variability between 1999 and 2007. Since 2008, however, biomass has been maintained at near record-low levels. The relatively high mean level of ninespine stickleback abundance during 1996-2007 has been attributed to dreissenid mussels somehow enhancing ninespine stickleback spawning and nursery habitat, perhaps through proliferation of *Cladophora* (Madenjian et al. 2010b). One plausible explanation for the low ninespine stickleback abundance during 2008-2013 is that piscivores have begun to incorporate ninespine

sticklebacks into their diets as the abundance of alewives has remained at a low level. Jacobs et al. (2013) found ninespine sticklebacks to be a rare diet item (i.e., 2% occurrence) among large Chinook salmon in 2009-2010 after a 0% occurrence in 1994-1996.

LAKE-WIDE BIOMASS

We estimated a total lake-wide biomass of prey fish available to the bottom trawl in 2013 of 43 kilotonnes (kt) (1 kt = 1000 metric tonnes) (Figure 8a, Appendix 1). Total prey fish biomass was the sum of the population biomass estimates for alewife, bloater, rainbow smelt, deepwater sculpin, slimy sculpin, ninespine stickleback, and round goby. Total prey fish biomass in Lake Michigan has trended downward since 1989, primarily due to a dramatic decrease in bloater biomass (Figure 8a). During 2002-2012, decreases in alewife and deepwater sculpin biomasses also contributed to the continued decrease in total prey fish biomass. Total biomass first dropped below 30 kt in 2007, and remained below 30 kt during 2007-2012, but then increased to 43 kt in 2013. This increase must be interpreted with caution, however, due to the high degree of uncertainty in the 2013 biomass estimates for alewife and round goby.

As Figure 8b depicts, the 2013 prey fish biomass was apportioned as: alewife 67.0% (29.0 kt), round goby 25.0% (10.8 kt), bloater 3.7% (1.6 kt), deepwater sculpin 3.1% (1.3 kt), slimy sculpin 0.7% (0.3 kt), rainbow smelt 0.5% (0.2 kt), and ninespine stickleback < 0.1% (0.004 kt).

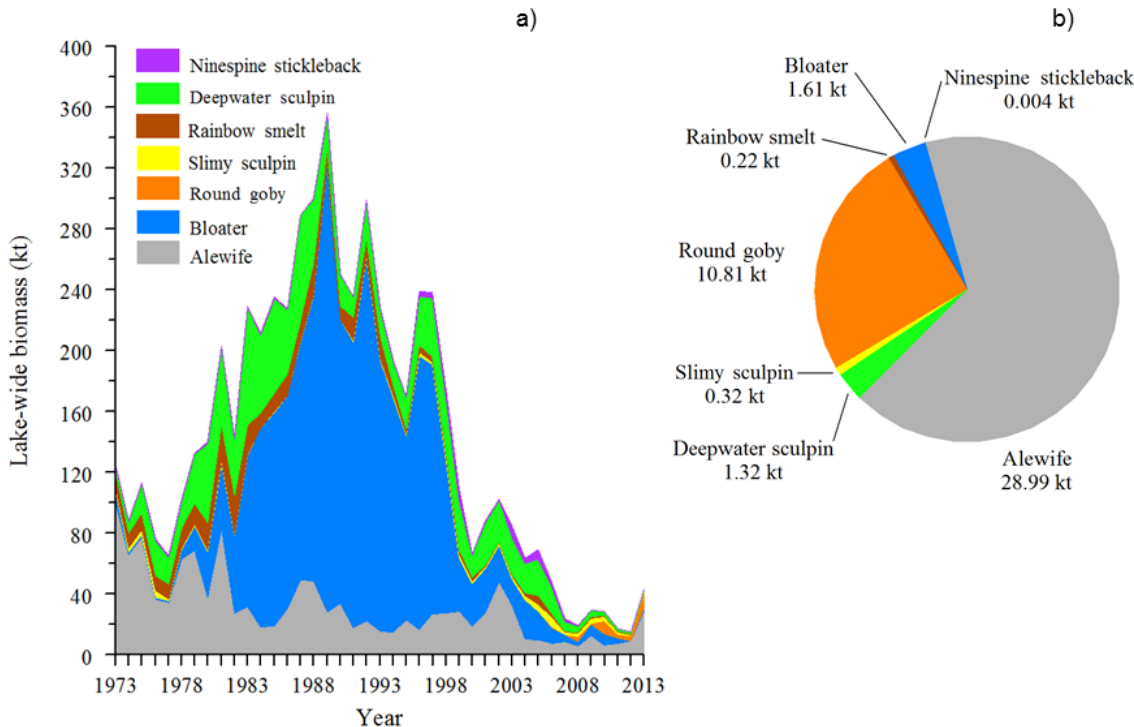


Figure 8. Estimated lake-wide (i.e., 5-114 m depth region) biomass of prey fishes in Lake Michigan, 1973-2013 (a) and species composition in 2013 (b).

OTHER SPECIES OF INTEREST

Burbot – Burbot and lake trout represent the native top predators in Lake Michigan. The decline in burbot abundance in Lake Michigan during the 1950s has been attributed to sea lamprey predation (Wells and McLain 1973). Sea lamprey control was a necessary condition for recovery of the burbot population in Lake Michigan, however Eshenroder and Burnham-Curtis (1999) proposed that a reduction in alewife abundance was an additional prerequisite for burbot recovery.

Burbot collected in the bottom trawls are typically large individuals (>350 mm TL); juvenile burbot apparently inhabit areas not usually covered by the bottom trawl survey.

Burbot biomass density was 0.1 kg per ha in 2013, which was 13% of the long-term average. After a period of low numeric density in the 1970s, burbot showed a strong recovery in the 1980s (Figure 9a). Densities increased through 1997, but declined thereafter. Perhaps the apparent decrease in burbot abundance during 2007-2013 was due to a portion of the burbot population moving to waters deeper than 110 m in response to a movement of deepwater sculpins, favored prey of burbot (Van Oosten and Deason 1938; Gamble et al. 2011), to deeper waters.

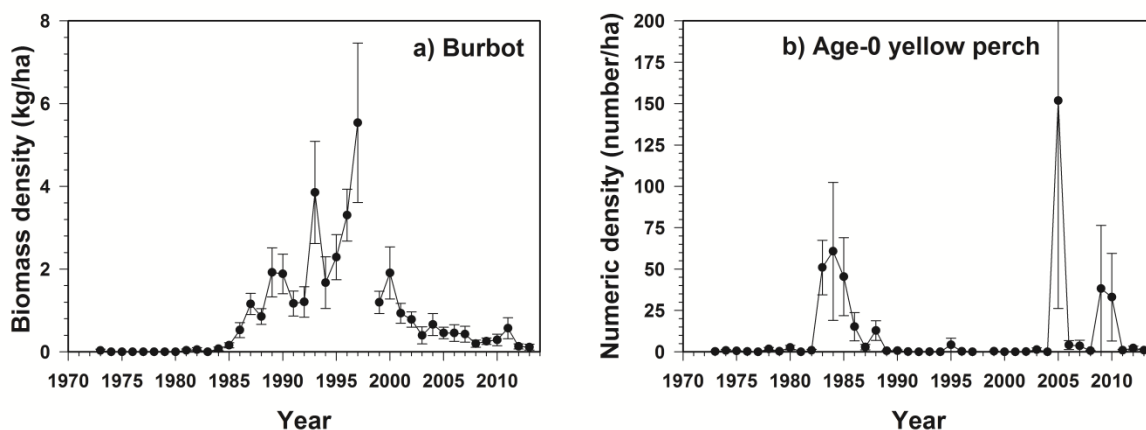


Figure 9. Biomass density (+/- standard error) of burbot (a) and numeric density (+/- standard error) of age-0 yellow perch (b) in Lake Michigan, 1973-2013.

Age-0 yellow perch – The yellow perch population in Lake Michigan has supported valuable recreational and commercial fisheries (Wells 1977). GLSC bottom trawl surveys provide an index of age-0 yellow perch numeric density, which serves as an indication of yellow perch recruitment success. The 2005 year-class of yellow perch was the largest ever recorded (Figure 9b) and the 2009 and 2010 year-classes also were higher than average. Strong yellow perch recruitment in these recent years was likely attributable to a sufficient abundance of female spawners and favorable weather (e.g., Makauskas and Clapp 2000). Numeric density of the 2013 year-class was only 1 fish per ha, indicative of a relatively weak year-class.

Dreissenid mussels – The first zebra mussel (*Dreissena polymorpha*) noted in Lake Michigan was found in May 1988 in Indiana Harbor at Gary, Indiana. By 1990, adult mussels had been found at multiple sites in the Chicago area, and by 1992 were reported to range along the eastern and western shoreline in the southern two-thirds of the lake, as well as in Green Bay and Grand Traverse Bay (Marsden 1992). In 1999, catches of dreissenid mussels in our bottom trawls became significant and we began recording biomass for each tow. Lake Michigan dreissenid mussels include two species: the zebra mussel and the quagga mussel. The quagga mussel is a more recent invader to Lake Michigan than the zebra mussel (Nalepa et al. 2001). According to the GLSC bottom trawl survey, biomass density of dreissenid mussels was highest in 2007 (Figure 10a), which followed an exponential like increase between 2004 and 2006 (Bunnell et al. 2009b). The biomass density of dreissenid mussels in 2013 was 6.6 kg per ha (Figure 10a). Interannual variability in dreissenid mussel density following 2007 is difficult to explain. The exceptionally high densities in 2006 and 2007 were attributable to the expansion of quagga mussels into deeper (> 60 m) waters of Lake Michigan. However, there was no clear explanation for the drastic drop in dreissenid mussel biomass density between 2007 and 2008. According to the results of the benthic macroinvertebrate survey led by Tom Nalepa at NOAA-GLERL, quagga mussel biomass density in Lake Michigan appears to have peaked sometime between 2008 and 2010. This peaking may be in response to the exceeding of the carrying capacity, and a decline in quagga mussel biomass density may be expected in upcoming years.

Over this same period of dreissenid mussel increases, prey fish biomass was declining, which led to a dramatic increase in the percentage of dreissenids in the total bottom trawl catch (Figure 10b). Some authors have attributed the recent decline in prey fish to food-web changes induced by the expansion of dreissenids (Nalepa et al. 2009). However, Bunnell et al. (2009b) proposed that the bulk of the decline in total prey fish biomass may be better explained by factors other than food-web-induced effects by dreissenids, including poor fish recruitment (that preceded the mussel expansion), shifts in fish habitat, and increased fish predation by Chinook salmon and lake trout.

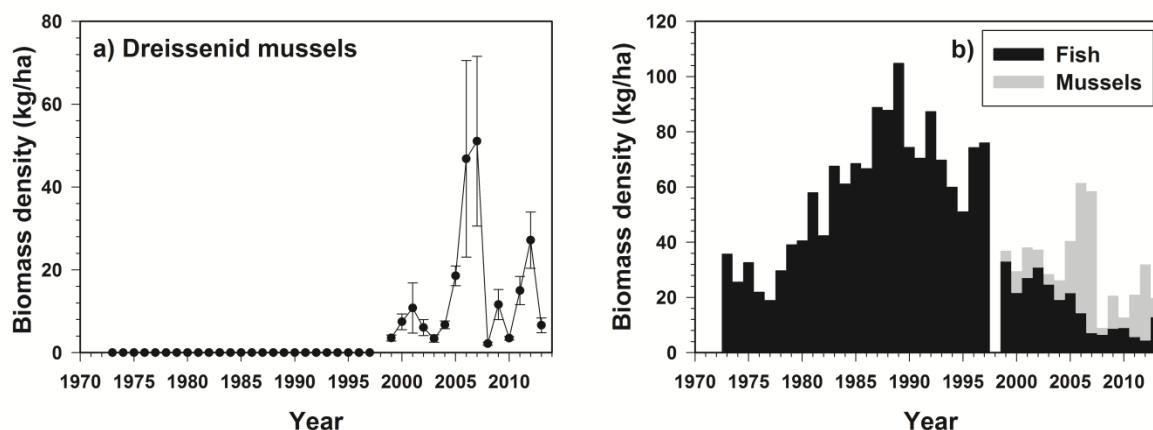


Figure 10. Panel (a) depicts biomass density (+/- standard error) of dreissenid mussels in the bottom trawl in Lake Michigan between 1999 (first year mussels were weighed) and 2013. Panel (b) depicts biomass of dreissenids and total fish biomass estimated by the bottom trawl between 1973 and 2013.

A comparison of the biomass density of dreissenid mussels (6.6 kg per ha) with biomass density of all species of fish (13 kg per ha) caught in the bottom trawl in 2013 indicated that 34% of the daytime benthic biomass available to the bottom trawl was dreissenid mussels (Figure 10b).

CONCLUSIONS

Although total prey fish biomass in 2013 was higher than that estimated for years 2007-2012, total prey fish biomass was still relatively low during 2013. Further, uncertainty in the 2013 total prey fish biomass estimate was extremely high. Prudently, we conclude that, based on the bottom trawl survey results, total prey fish biomass in Lake Michigan has remained at a low level during 2007-2013. This low level of prey fish biomass was attributable to a suite of factors, two of which can be clearly identify as: (1) a prolonged period of poor bloater recruitment since 1992 and (2) intensified predation on alewives by Chinook salmon during the 2000s. Adult alewife density has been maintained at a relatively low level over the last 10 years and the age distribution of the adult alewife population has become especially truncated in recent years. As recent as 2007, alewives as old as age 9 were sampled in this survey whereas the oldest alewife sampled in 2013 was age 5. Whether or not the alewife population in Lake Michigan will undergo a collapse in coming years (similar to what occurred in Lake Huron) will depend on several factors. Primarily, the extent to which predation by salmonines influences the survival of the large 2010 alewife year-class is critical. Salmonine predation on the 2012 alewife year-class will also be important. In addition, alewife sustainability will depend on the ability of alewife spawning stock to produce another strong year-class in the next few years, which will at least partially depend on appropriate environmental factors being met (Madenjian et al. 2005b).

According to the bottom trawl survey estimates, native fishes represented only 7.5% of the total prey fish biomass in Lake Michigan in 2013. Native deepwater sculpin and ninespine stickleback were at record-low levels in 2013, biomass of native slimy sculpin continued a 4-year downward trend in 2013, and biomass of native bloater remained low in 2013. When interpreting the bottom trawl survey results, the

possibility that two of these native species, deepwater sculpin and bloater, shifted their habitat use to deeper waters during recent years should be considered. If this shift did indeed occur, then the bottom trawl estimates for these two fishes may represent extreme underestimates of their biomass in Lake Michigan.

Scientists and managers continue to ask critical questions regarding the importance of “bottom-up” effects on prey fish biomass in Lake Michigan. For example, to what extent do (1) ongoing declines in total phosphorus (Evans et al. 2011), (2) the proliferation in dreissenid mussels, and (3) the resultant diminishment of the spring phytoplankton bloom (Fahnenstiel et al. 2010) reduce the capacity of Lake Michigan to produce the biomass of prey fish that was observed only two decades ago? We point out that the Lake Michigan ecosystem has already demonstrated its capacity to produce a strong year-class of alewives in 2010 despite the changes described above. Nonetheless, having a complete understanding of the answers to these questions will require additional years of surveillance, across-lakes comparisons, and food-web analyses.

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Appendix 1. Mean numeric and biomass density, as well as lake-wide biomass (defined as biomass available to the bottom trawls for the region of the main basin between the 5-m and 114-m depth contours) estimates for various fishes and dreissenid mussels in Lake Michigan during 2013. Estimates are based on the bottom trawl survey. Standard error enclosed in parentheses. NA denotes that estimate is not available.

Taxon	Numeric density (fish per ha)	Biomass density (kg per ha)	Lake-wide biomass (kt)
age-0 alewife	3.01 (2.20)	0.016 (0.012)	0.056 (0.042)
adult alewife	417.42 (355.80)	8.216 (7.083)	28.933 (24.943)
age-0 bloater	6.01 (2.79)	0.048 (0.023)	0.169 (0.080)
adult bloater	9.89 (3.32)	0.408 (0.206)	1.438 (0.724)
age-0 rainbow smelt	10.75 (6.73)	0.011 (0.009)	0.039 (0.030)
adult rainbow smelt	8.73 (7.66)	0.052 (0.046)	0.183 (0.161)
deepwater sculpin	38.86 (11.79)	0.375 (0.124)	1.321 (0.436)
slimy sculpin	17.47 (4.76)	0.090 (0.024)	0.318 (0.084)
ninespine stickleback	0.80 (0.39)	0.001 (0.001)	0.004 (0.002)
Burbot	0.07 (0.04)	0.112 (0.070)	0.395 (0.247)
age-0 yellow perch	0.91 (0.91)	0.002 (0.002)	0.008 (0.008)
round goby	230.64 (201.60)	3.069 (2.890)	10.807 (10.179)
dreissenid mussels	NA	6.588 (1.798)	23.201 (6.331)